BREEDING BIOLOGY OF SNOWY PLOVERS AT GREAT SALT LAKE, UTAH

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ABSTRACT.—I studied the breeding behavior of Snowy Plovers (*Charadrius alexandrinus*) in northern Utah from 1990–1993. Nests at Great Salt Lake were initiated over a 14-week period from mid-April to mid-July, and were more comparable to data from California than from Kansas. Breeding males were first resighted from late March through May, whereas females had a more prolonged arrival period from late March through mid-June (N = 256 color-banded adults). Renesting following nest loss was documented only twice, in part because birds often left the study sites. Most females departed immediately after nests hatched, while males exhibited uniparental care of broods. A similar mating system was described for coastal California, where sequential polyandry was documented regularly. During this study double-brooding and sequential polyandry were rarely observed, but both strategies were probably more common than I detected. Mayfield-method estimates of annual nest success ranged from 5.4% to 49.2%, with most nest failures apparently caused by mammalian predators. These results suggest that the breeding strategies of migratory plovers in Utah resemble those of resident and migratory birds nesting in California and Oregon, rather than migratory plovers nesting in the Great Plains. *Received 11 April 1994, accepted 15 Nov. 1994.*

The breeding behavior of Snowy Plovers (*Charadrius alexandrinus*) appears to vary among geographic regions. Warriner et al. (1986) found that plovers nesting in California were double-brooded and sequentially polygamous, while individuals in Kansas were single-brooded and mo- nogamous (Boyd 1972). In coastal California, both sexes shared incuba- tion duties, but males usually exhibited uniparental care of broods once eggs hatched (Warriner et al. 1986). While males remained with broods, females found new mates and initiated second clutches. If young fledged early in the breeding season, males initiated second clutches with new females. In contrast, plovers in Kansas had biparental care of broods (Boyd 1972). A small percentage of European Kentish Plovers (*C. a. alexandrinus*) also exhibit sequential polyandry (Rittinghaus 1956, Szék- ely and Lessells 1993).

Studies of Snowy Plover breeding biology in western North America have focused on populations of Oregon and California (Page et al. 1983, 1985; Wilson-Jacobs and Meslow 1984; Warriner et al. 1986). The most comprehensive study was in coastal California, where many birds in the population were year-round residents (Warriner et al. 1986). Little is known about its breeding biology in the eastern Great Basin, where birds

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are all migratory (Page et al. 1995). There is a need to examine Snowy Plover breeding biology throughout its range because Pacific Coast populations were listed as threatened by the U.S. Fish and Wildlife Service in April 1993 (Federal Register 1993). I report on the migratory and nesting chronology, mating system, and nest success of Snowy Plovers at Great Salt Lake, Utah.

STUDY AREA AND METHODS

I studied Snowy Plovers at two study sites at Great Salt Lake, Davis County, Utah, from 1990 to 1993: Howard Slough Waterfowl Management Area (350 ha; 41°09′N, 112°09′W) and West Layton marsh (400 ha; 41°02′N, 112°05′W). These sites are approximately 10 km apart on the eastern, central shore of the lake. The Utah Division of Wildlife Resources (UDWR) actively manages Howard Slough for waterfowl production using a series of diked impoundments. UDWR personnel controlled mammalian predators at Howard Slough (red fox [*Vulpes vulpes*], striped skunk [*Mephitis mephitis*], and raccoon [*Procyon lotor*]). West Layton marsh (hereafter Layton marsh) is jointly owned and managed by UDWR and the Nature Conservancy, and predators were not controlled at this site. Layton marsh is part of the lake's largest complex of undiked wetlands. Both study sites were dominated by salt flats, interspersed with patches of salt-tolerant plants of the family Chenopodiaceae, including greasewood (*Sarcobatus vermiculatus*), iodine bush (*Allenrolfea occidentalis*), seepweed (*Suaeda* spp.), summer cypress (*Kochia scoparia*), bassia (*Bassia hyssopifolia*), and pickleweed (*Salicornia europaea*). In addition, marsh vegetation increased dramatically over the course of the study and consisted primarily of alkali bulrush (*Scirpus maritimus*), cattail (*Typha* spp.), and phragmites (*Phragmites australis*) (Paton 1994).

From 1990 through 1993, we surveyed study sites at least twice weekly from 15 March through 31 August. Surveys were initiated at Howard Slough on 4 May and at Layton marsh on 13 June in 1990. I worked by myself in 1990 and had one field assistant from 1991 to 1993. We located nests using the nest-searching techniques of Page et al. (1985). Expected hatching dates were determined by floating the eggs (Westerkov 1950) and assuming an egg-laying period of four days and a 27-day incubation period (Warriner et al. 1986, Page et al. 1985). I considered nests successful if at least one chick hatched. Nests were classified as unsuccessful if they were empty prior to expected hatching dates (69.1% of 175 depredated nests), if obvious predator signs were found at nests (18.9%), or if small egg shell fragments (indicating pipping) were absent from the scrape lining after the expected hatching dates (12%). I calculated apparent nest success (i.e., number of successful nests divided by the total number of nests) and Mayfield-method estimates of nest success (i.e., success based on exposure days; Mayfield 1961, Johnson 1979, Johnson and Shaffer 1990). Only nests active for at least one week were used in analyses of clutch size because the egg-laying period can take up to five days (Warriner et al. 1986). Following Page et al. (1983), I defined fledglings as the age class when juveniles were capable of flight. Fledging success was estimated from the mean size of broods at four weeks post-hatching (Page et al. 1983, Warriner et al. 1986).

I captured incubating plovers with a circular funnel trap, or herded them into two mist nets staked together to form a 'V'. Plovers were uniquely marked with four unicolored legbands. We banded 82 adults and 60 immatures (i.e., where immature equals both chicks and fledglings) at the sites in 1990, 142 adults and 22 immatures in 1991, and 137 adults and 79 immatures in 1992.

Nesting chronology was analyzed by pooling data into ten 15–16 day long periods, from

1 April to 31 August (e.g., 1–15 May, 16–31 May). A likelihood ratio chi-square test (G^2) was then used to compare the goodness-of-fit between the two study sites and among years at the same study site. To determine how long individual plovers remained at the study sites, I used only birds resighted in years subsequent to their initial banding year. I divided these data into two groups: (1) definite breeding individuals because they were captured or observed on a nest (nest confirmed) and (2) birds seen at the focal study sites but never associated with a nest (no nest confirmed). I also calculated the number of days birds remained at the study sites following nesting failure or success. This latter analysis included birds banded in the preceding years and their banding year.

To monitor daily movements of foraging color-banded adults away from their active nests, we conducted biweekly transect surveys of both study sites. We plotted observations of color-banded individuals on field maps (1 cm = 100 m); therefore, observations were accurate to within a 50 m radius of the actual location. Nests were mapped using a satellite-based global positioning system. I used a Mann-Whitney test to compare daily movement distances between the sexes. For this comparison, I used only the mean distance individuals moved within a breeding season to reduce pseudo-replication errors associated with multiple observations on the same bird. In all analyses, statistical significance was based on an alpha level equal to 0.05.

RESULTS

Migratory chronology.—Snowy Plovers began arriving in northern Utah in late March, with the earliest sighting on 19 March 1992. The migratory chronology of adult males differed significantly from that of females ($G^2 = 23.9$, 10 df, $P = 0.008$). Breeding males appeared to arrive during two peak periods; there was a large influx of birds from late March to 31 May and a small peak centered on 1–15 July (Fig. 1). In contrast, confirmed breeding females had an extended arrival period from late March to mid-June. Some banded adult males and females were not resighted at the study sites until late July, suggesting they possibly nested elsewhere that year or were simply transients.

Data on fall departure dates were not complete, as many juveniles were still in northern Utah after systematic fieldwork ended on 31 August. Immature plovers tended to congregate in large feeding flocks during August and September, with up to 350 birds observed in some flocks. Adults accounted for 12.8% of observations (N = 619) during systematic surveys after 15 August, whereas even fewer adults were seen during incidental observations in September (i.e., 2.3% of 608 individuals). I know of no October or November Snowy Plover records in Utah, although there is one record of a Snowy Plover on the south shore of Great Salt Lake in mid-December (C. Kneedy, Utah Ornithological Society, unpubl. data).

Nest chronology.—The egg-laying period usually commenced in the second week of April and continued as long as 14 weeks until the third week of July (range = 10 April–18 July; Fig. 2). As would be expected, given typical climatic variation, there was significant annual variation in
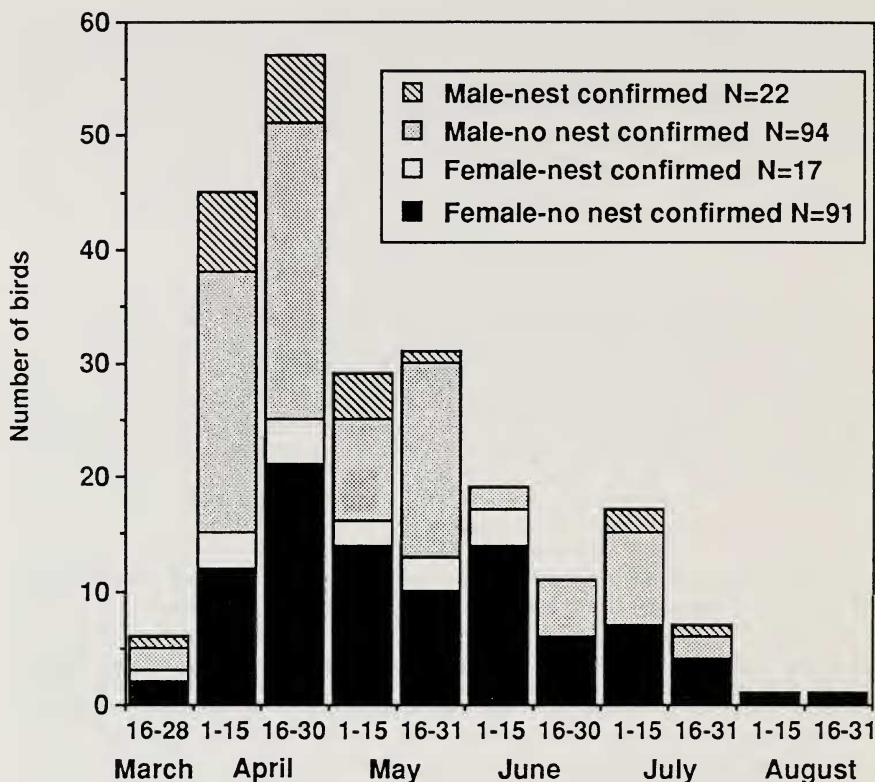
FIG. 1.   Arrival dates for confirmed breeding and potentially non-breeding Snowy Plovers (no nest confirmed) at Great Salt Lake.

nest chronology, with the nest initiation chronology differing significantly among years at both Howard Slough (G^2 = 29.1, 14 df, P = 0.01) and Layton marsh (G^2 = 29.7, 14 df, P < 0.001). The timing of nest initiations differed between the two sites in 1991 (G^2 = 15.1, 6 df, P = 0.020) and 1992 (G^2 = 19.8, 7 df, P = 0.006) but not in 1993 (G^2 = 7.0, 7 df, P = 0.43).

Breeding adult males had a tendency to be observed for more days than adult females during the breeding season, although this difference was not statistically significant (Mann-Whitney U-test, P = 0.082) (Fig. 3). Breeding female plovers were seen a median of 45 days (25%–75% quartiles = 33–65, maximum = 98 days, N = 17), whereas breeding males were observed a median of 53.5 days (25%–75% quartiles = 39–80, maximum = 149 days, N = 22).

Both sexes left the study sites immediately following nest failure and
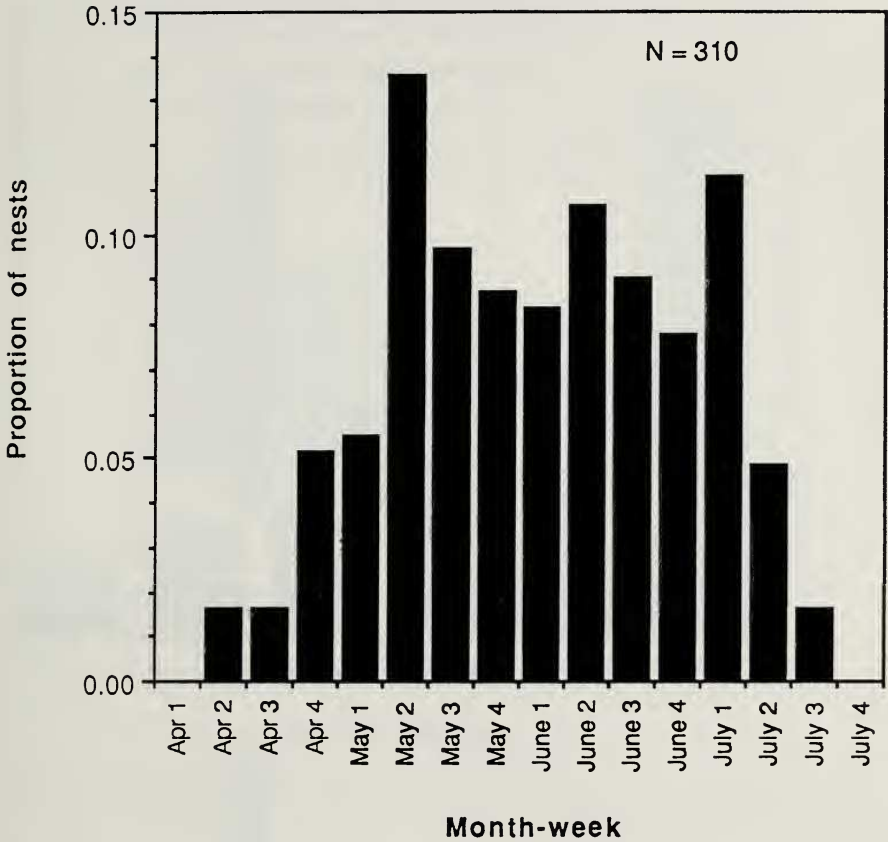
FIG. 2.   Nest initiation chronology for Snowy Plovers at Great Salt Lake.

were not subsequently resighted that year (41.5% of 41 females, 46.4% of 28 males; G^2 = 0.17, 1 df, P = 0.68; Fig. 4). A substantial number of unsuccessful breeding birds were detected for $\geq$50 days at the same study site (i.e., 29.3% of 41 females and 28.5% of 28 males). However, I only documented the same pair renesting together twice following clutch loss.

Males tended to be detected for longer time periods than females after nests successfully hatched (G^2 = 17.5, 4 df, P = 0.002) (Fig. 4). The majority of females (57.5% of 47) were not resighted two days after eggs hatched, and only a small percentage of the successful females (16.9% of 47) remained at the study sites for over 25 days. In contrast, most males (63.8%) were observed at the study sites for at least 11 days with their broods. A substantial number of males (23.4%) were not resighted
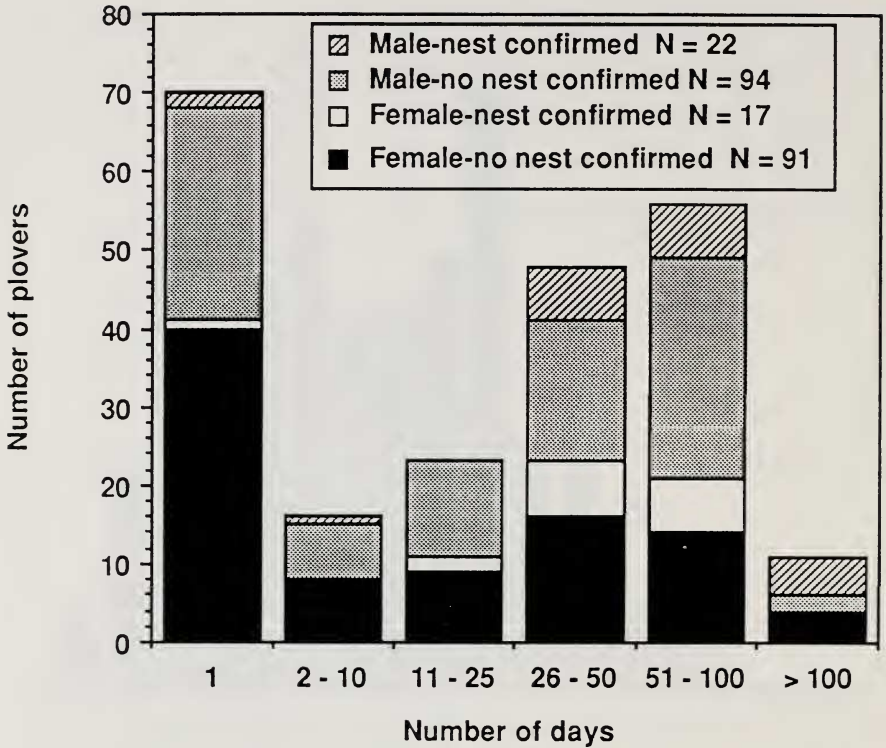
FIG. 3. Number of days that adult Snowy Plovers were detected at study sites during the breeding season. Data are shown by sex for potentially non-breeding birds (no nest confirmed) and breeding birds (nest confirmed).

two days after nests hatched, apparently because they led their broods off the study sites.

Incubation behavior.—Snowy Plovers at Great Salt Lake appeared to defend a relatively small area immediately around the nest (i.e., 10–20 m radius around the nest). Nonincubating parents foraged in areas separate from nest sites, and I rarely observed those birds foraging near nesting areas. Based on observations of color-banded birds known to be associated with active nests, I found that some plovers travelled over 3 km to foraging sites (Fig. 5). Females were found as far as 3770 m from active nests (median = 177 m, 25%–75% quartiles = 64–466 m, N = 192

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FIG. 4. Number of days that adult Snowy Plovers were detected at study sites after nests hatched (successful) or failed (unsuccessful).
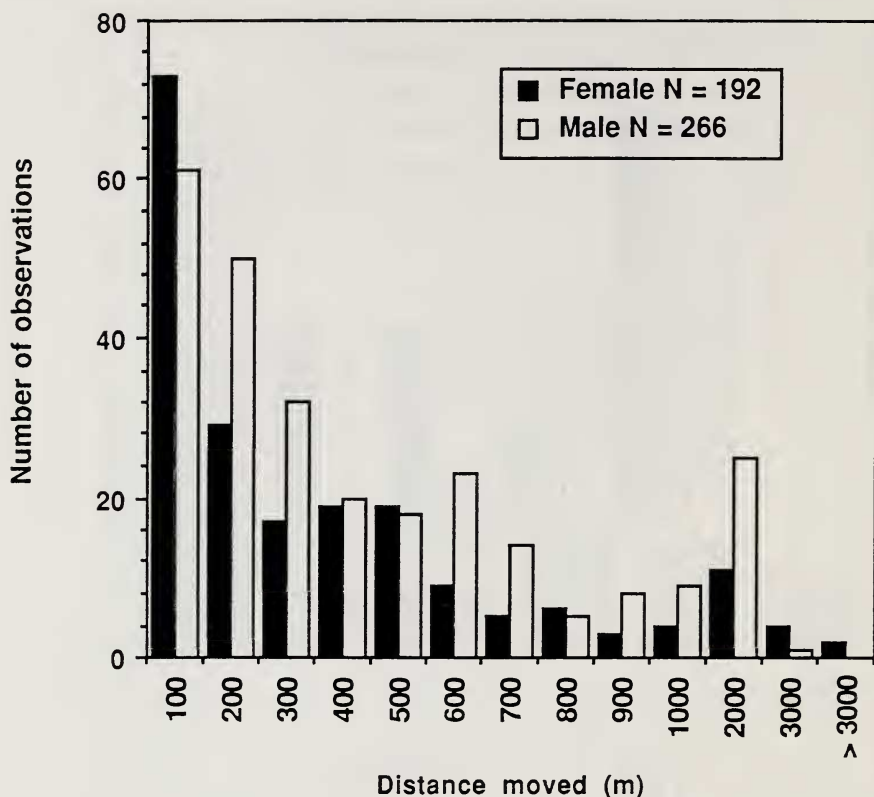
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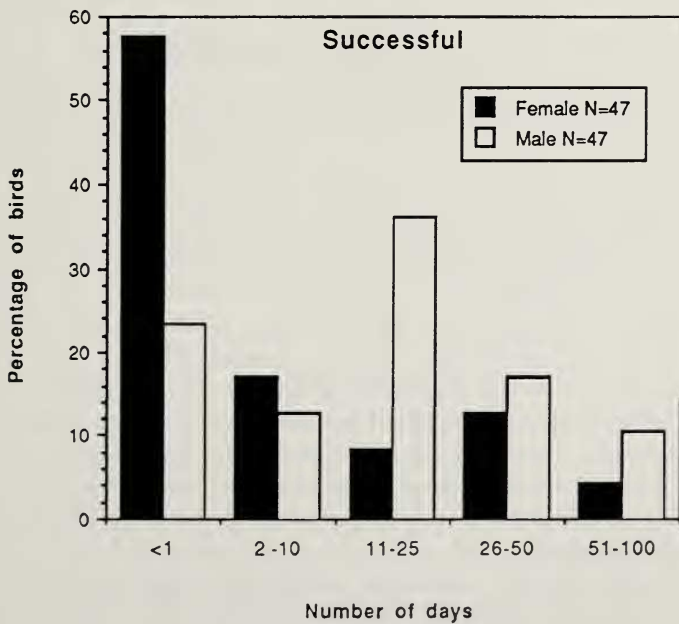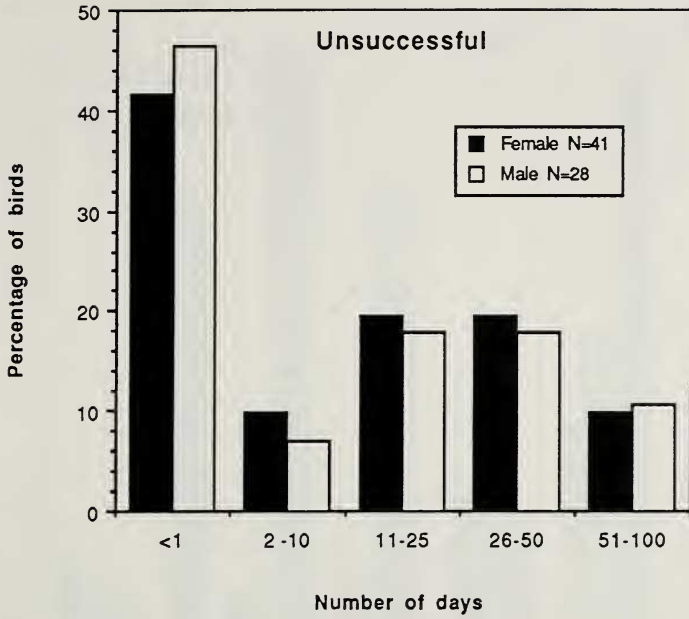
FIG. 5.   Distances travelled by foraging or roosting Snowy Plovers away from active nests.

observations), while males were found as far as 2030 m (median = 272 m, 25%–75% quartiles = 110–580 m, N = 266). There was no intersexual variation in distances travelled (Mann-Whitney U-test = −1.2, N_1 = 60, N_2 = 53, P = 0.22) (Fig. 5).

The daytime incubation chronology differed between the sexes (G^2 = 23.2, 6 df, P = 0.001; Fig. 6). Females tended to incubate during the morning hours, while males often incubated in the mid-afternoon and late evening. Males and females often would exchange incubation duties on hot afternoons at short intervals (i.e., 10–15 min). In addition, males often would relieve females at dusk, when females were observed foraging together in small flocks. No attempts were made to quantify nocturnal incubation behavior.

Clutch size.—Modal clutch size was three eggs (93.3% of 327 clutches). There were 18 nests with a clutch size of two eggs, three nests
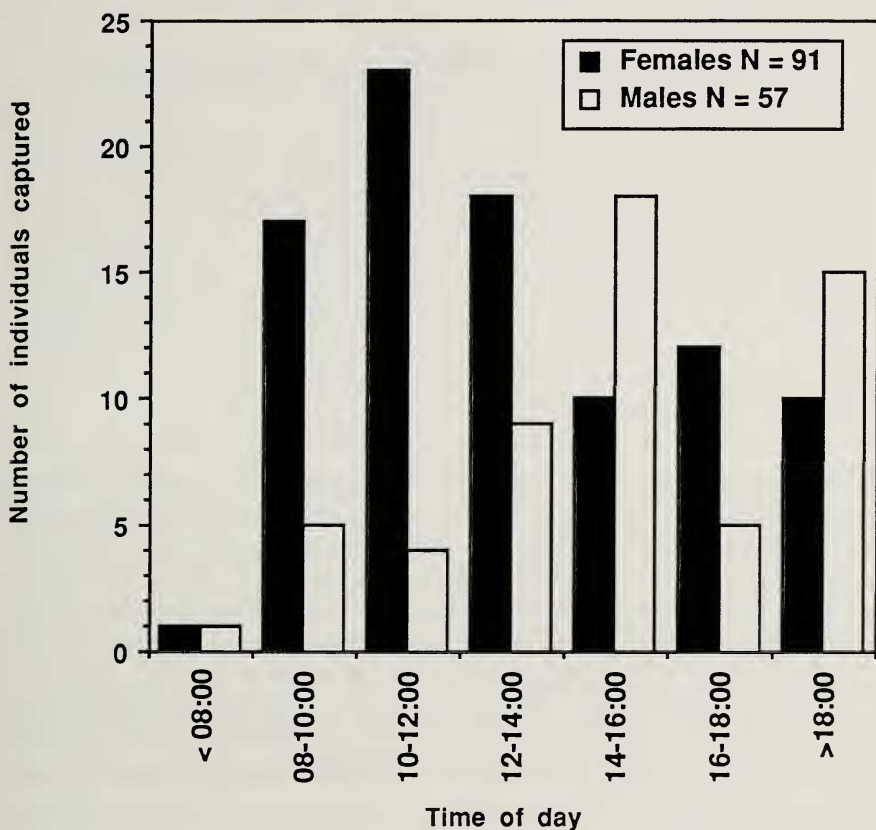
FIG. 6.   Intersexual variation in daily incubation chronology of Snowy Plovers based on capture times of incubating adults.

with four eggs, and one nest with five eggs. There was no annual variation in clutch size over the four years of the study ($G^2 = 7.5$, 9 df, $P = 0.58$), and clutch size was similar between the two study sites ($G^2 = 2.3$, 3 df, $P = 0.52$).

Pair retention, double-brooding and polyandry.—Snowy Plovers in Utah did not exhibit mate fidelity between years. I documented only one occasion when the same pair remated between years, based on 123 nest attempts for 30 pairs initially banded. The pair that remated was originally banded at Layton on an unsuccessful nest in 1990. In 1991, the female mated with another male at Howard Slough, while the original male was seen only once at Layton marsh. In 1992, the 1990 pair successfully nested together at Howard Slough.

I twice documented double-brooding within the same year. One banded

	Howard Slough				Layton Marsh			
	Mayfield method[a]		Apparent success	N	Mayfield method		Apparent success	N
Year	Mean	95% CI			Mean	95% CI		
1990	0.492	0.27–0.84	0.611	18	0.381	0.28–0.59	0.623	53
1991	0.197	0.10–0.38	0.314	35	0.113	0.06–0.20	0.247	73
1992	0.445	0.33–0.59	0.594	79	0.129	0.07–0.24	0.236	55
1993	0.054	0.11–0.17	0.133	30	0.345	0.17–0.70	0.471	71

[a] Based on Mayfield (1961) and Johnson (1979).

male at Layton marsh (mated with an unbanded female) had a clutch hatch successfully on 5 May 1991 and was last seen with this brood on 24 May. This male was then observed building a scrape on 7 June and incubating a second clutch, with an unbanded female, from 13 June to 10 July. Since neither female was banded, I do not know if the female represented one or two individuals. In the other instance, the one-day-old brood of a banded pair died after a cold rainstorm at Howard Slough on 8 May 1993. The female remated with a new banded male, although her original mate was still alive, and initiated a second nest on 10 June. This second clutch was lost to a predator on 20 June. This latter case was also the only example of within-year sequential polyandry I documented during this study.

Nest success.—Estimates for mean annual nest success (Mayfield method) ranged from 5.4 to 49.2% at Howard Slough and 11.3 to 38.1% at Layton marsh (Table 1). Nest success varied widely from year to year, and the annual fluctuations were not consistent between the two study areas ($G^2 = 43.5$, 3 df, $P < 0.001$; Table 1). Mammalian predators were responsible for most nest failures (42%, N = 188) based on tracks and scat near nests. Avian predators were documented taking 6.9% of all nests, flooding totalled 13.8% of nest losses, and unknown predators (37.3%) accounted for the remainder of the losses. I often could not determine the type of predator because both mammalian and avian predators will remove eggs from nests (Rearden 1951; G. Page, pers. comm.), and the soil was usually too hard for track retention. However, red foxes were probably the primary predators during this study, accounting for 90% of all documented mammalian nest depredations, and because red foxes were the most common predator at both study sites all four years. Striped skunks were observed only in 1993, and raccoons were also rare until

TABLE 2

ANNUAL VARIATION IN AVERAGE SNOWY PLOVER BROOD SIZE BY AGE CLASS

Age[a]	1990		1991		1992		1993		F[b]	P
	$\bar{x} \pm SE$	N	$\bar{x} \pm SE$	N	$\bar{x} \pm SE$	N	$\bar{x} \pm SE$	N		
1	2.3 ± 0.1	50	2.3 ± 0.1	49	2.3 ± 0.1	53	2.1 ± 0.2	23	0.2	0.89
2	2.3 ± 0.1	22	2.2 ± 0.2	36	2.1 ± 0.1	71	2.0 ± 0.2	36	0.9	0.42
3	2.2 ± 0.2	18	1.9 ± 0.2	27	2.1 ± 0.1	50	2.0 ± 0.2	31	0.5	0.66
4	2.0 ± 0.1	57	1.9 ± 0.1	36	1.8 ± 0.1	54	1.8 ± 0.1	57	0.7	0.56

[a] Brood age in weeks.
[b] ANOVA, comparing brood size among years by brood age.

1993. California Gulls (*Larus californicus*) appeared to prey on plover nests only where gulls roosted, and I never observed gulls actively searching for plover nests. Common Ravens (*Corvus corax*) depredated ten nests, all at Layton marsh, where flocks of up to 65 ravens were occasionally observed foraging in plover nesting habitat. In contrast, ravens were rarely observed foraging at Howard Slough.

Fledging success.—There was no apparent annual variation in the number of chicks in the four age classes (Table 2), and fledging rates did not appear to vary annually with an average of 1.87 chicks per brood for successful nests (Table 2). I had a relatively difficult time following individual broods for long periods of time. Therefore, I was unable to estimate the percentage of broods that did not successfully fledge any young.

DISCUSSION

The duration of the breeding season for Snowy Plovers nesting in Utah (14 weeks) was closer in length to that reported from coastal California (Warriner et al. 1986) than from Kansas (Boyd 1972, Grover and Knopf 1982). Plovers breeding in Utah are all migratory (Page et al. 1995). In contrast, Snowy Plover populations in coastal California consist of both migratory and year-round resident birds and have egg-laying periods encompassing 16 weeks from 23 March to 13 July (Warriner et al. 1986). Birds nesting in the Great Plains are also migratory, and most nests are initiated during a six-week period from 15 May to 30 June; there is one early record from 22 April (Boyd 1972, Grover and Knopf 1982). Given the relatively short breeding season in the Great Plains, it is not surprising that birds breeding there appear to be exclusively single-brooded and monogamous (Boyd 1972).

The mating system of Snowy Plovers breeding in northern Utah appears to resemble that of coastal California populations (Warriner et al.

1986; Stenzel et al. 1994) more than those in the Great Plains (Boyd 1972, Grover and Knopf 1982). Four lines of evidence suggest that Snowy Plovers nesting in Utah are regularly double-brooded and sequentially polygamous, although I found little direct evidence to support the existence of either strategy at Great Salt Lake. First, I documented two examples of double-brooding. Second, plovers in Utah exhibited uniparental care of broods, with only males taking care of broods one week after hatching. Third, based on a 31-day laying and incubation period (Page et al. 1985, Warriner et al. 1986) and the fact that only males care for broods, there was ample time for females to produce two clutches during the 14-week nest initiation period in northern Utah. Finally, the nest initiation chronology suggests there are two or three distinctive peak initiation periods (Fig. 2). Based on studies conducted in California, the peak during the second week of June potentially represents successful females initiating second clutches, while the early July peak represents successful males initiating second clutches (G. Page, pers. comm.).

My inability to find the nests of the majority of the banded birds resighted at the study sites (i.e., 84.3% of 108 females, 81.0% of 116 males; Fig. 3) may have been due to at least five factors. First, an unknown percentage of both sexes could have been "floaters" (i.e., nonbreeding birds that did not nest that year; see Beletsky 1992). Second, many females and males (44.0% and 28.7%, respectively) were observed only on one occasion within a breeding season. This suggests that a substantial proportion of the plovers observed at the study sites were transients from other locations at Great Salt Lake or an even larger region, trying to find either suitable breeding habitat or potential mates. A similar strategy has been reported among Spotted Sandpipers (*Actitis macularia*), although their search for breeding sites appears to be more restricted to the post-breeding dispersal period (Reed and Oring 1992). Third, plovers in Utah often spent most of the day foraging over one km from their nests (Fig. 5), with the likely result that many nests went undiscovered. Fourth, breeding plovers were often extremely secretive around their nest (Boyd 1972, Warriner et al. 1986, Paton 1994). For example, three color-banded breeding adults (1 female and 2 males) were resighted only when they were captured on their nests but were not seen before or afterwards. Their secretive nature made it extremely difficult to determine which individual bird was associated with each nest. Finally, large numbers of plovers used each study site. This was exemplified by the fact that although I banded 256 adults at both sites, banded birds often accounted for less than ten percent of the birds observed on any given day (Paton 1994). Thus when nests were found, they were often those of unbanded birds.

In contrast to results from coastal California (Warriner et al. 1986),

Kansas (Boyd 1972) and the European subspecies in Germany (Rittinghaus 1956), I found little evidence that Snowy Plovers in northern Utah commonly renested in the immediate vicinity of their failed nest. Reasons for the apparent absence of renesting in Utah are unclear. It is possible that with so much plover nesting habitat available to breeding birds around Great Salt Lake from 1990 to 1993, pairs that attempted to renest moved off the study sites to maximize the probability of a successful nesting attempt. Snowy Plovers are known to be highly mobile, with females often moving over 50 km between nests (Stenzel et al. 1994). However, at most breeding sites in western North America, they are known to renest soon after clutch loss (G. Page, pers. comm.). This suggests that my inability to identify the owners of many nests was the primary reason I rarely documented renesting.

Apparent nest success rates found during this study (13.3%–62.3%) were lower than reported for plovers in Oklahoma (38–73%; Grover and Knopf 1982), Kansas (55%–60%; Boyd 1972), coastal California (50%; Warriner et al. 1986), and eastern, interior California (59.3%; Page et al. 1985). Of all these studies, Utah was the only area where red foxes were the dominant predator. A recent invasion of red foxes in coastal California has had a significant negative impact on plover nest success (G. Page, pers. comm.). Red foxes are the primary predator of Piping Plovers (*C. melodus*) nesting along parts of the Atlantic coast (Patterson et al. 1991) and have forced managers to adopt short-term solutions such as fencing off individual nests to reduce depredation problems (Rimmer and Deblinger 1990). However, long-term management strategies need to be developed to minimize nest depredation by red foxes on ground-nesting species throughout North America.

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